

Climate Change Estimates Surpass Rates of Climatic Niche Evolution in Primates

Andreas L. S. Meyer¹ & Marcio R. Pie²

¹ African Climate and Development Initiative, University of Cape Town, Cape Town, South Africa.

² Departamento de Zoologia, Universidade Federal do Paraná, CEP 81531-980 Curitiba, Paraná, Brazil.

Corresponding author: Andreas L. S. Meyer. E-mail: andreas.ls.meyer@gmail.com

ORCID

Andreas L. S. Meyer: 0000-0001-8870-5192

Marcio R. Pie: 0000-0002-2949-4871

Acknowledgments: We specially thank the guest editors Alejandro Estrada and Paul A. Garber for their efforts in bringing out this special issue. We also thank two anonymous reviewers for their valuable comments. ALSM is supported by a postdoctoral fellowship from the FLAIR Fellowship Programme: a partnership between the African Academy of Sciences and the Royal Society funded by the UK Government's Global Challenges Research Fund. MRP is supported by CNPq (Ministry of Science, Technology, and Innovation of Brazil), grant number 301636/2016-8.

Author contributions: ALSM and MRP conceived the ideas and designed the study; ALSM and MRP analyzed the data; ALSM led the writing.

Running head: Climatic Niches and Primate Adaptation

Abstract

Primates might be particularly vulnerable to experience adverse effects from climate change, given their level of exposure, sensitivity to climatic conditions, and biological traits associated with extinction proneness (e.g. low dispersal ability). Therefore, a key question is whether primates will be able to adapt fast enough to keep up with future climate change. In this study, we used phylogenetic comparative methods to estimate rates of climatic niche evolution for 293 species of primates. We then compare these with projected rates of future climate change. We show that for temperature-related variables, future rates are in general >2,800 times faster than rates of niche evolution characteristic of their recent evolutionary past. For precipitation-related variables, the overall difference between rates is >6,700. If emissions continue unabated, differences between past and future rates can be at least 4,800-fold for temperature-related variables and >7,900-fold for precipitation. Species occurring in Central South America, Central and Eastern Africa, Southeast Asia, and the Malay Archipelago are expected to experience the fastest rates of future climate change, relative to their past rates of climatic niche evolution. Our results suggest that primate adaptation to future climate change would require rates of niche evolution unparalleled in the recent history of the group. These findings reinforce the evidence that climate change is a major threat to primates worldwide.

Keywords: Ancestral Character States, Adaptation, Climate Change, Extinction, Niche Evolution, Phylogenetic Comparative Methods

Introduction

Anthropogenic climate change is already an important source of disturbance for the processes that structure and maintain biodiversity worldwide. Global mean temperatures raised ~ 1 °C since preindustrial times and projections suggest a further increase of at least 1.5 °C by 2100, even under high mitigation scenarios (IPCC 2014). Precipitation and wind regimes are also becoming more variable, increasing both the frequency and intensity of extreme climatic events (Coumou and Rahmstorf 2012; IPCC 2014). Such ongoing changes in climatic conditions are already triggering numerous responses in all levels of biodiversity, from organisms to ecosystems (Bellard et al. 2012; Lenoir et al. 2020; Pecl et al. 2017; Poloczanska et al. 2016). Although it is widely accepted that climate change will affect biodiversity globally, some taxa are likely to experience more pronounced impacts than others. This is the case of primates (Estrada et al. 2017; Korstjens and Hillyer 2016; Meyer 2017).

The higher vulnerability of primates to climate change has several causes. Firstly, most primate species will be exposed to conditions beyond their current thermal amplitudes. For instance, evidence from studies using ecological niche modeling suggest that many species will lose climatically suitable habitats from the middle of the present century onward (Brown and Yoder 2015; Hill and Winder 2019; Meyer et al. 2014; Sales et al. 2020). Furthermore, a global-scale analysis with >400 primate species revealed that the group, as a whole, might experience more warming than the global average (Graham et al. 2016). It is also important to note that most primate taxa inhabit tropical biomes, which are disproportionately sensitive to climate change (Newbold et al. 2020). Tropical regions are also projected to have more species exposed to temperatures beyond their realized niche limits when compared to other regions (Trisos et al. 2020),

and forest-dwelling primates are more likely to experience those unprecedented conditions (Carvalho et al. 2019; Stewart et al. 2020). Indeed, a recent study revealed that primates are among the mammals with the highest proportion of species predicted to have experienced adverse effects from recent climatic changes (Pacifiçi et al. 2017). Synergistic effects with other threats, such as land-use change, disease transmission, and hunting may exacerbate the vulnerability of the group, which could amplify population declines (Barrett et al. 2013; Carvalho et al. 2019; Gouveia et al. 2016).

Another important dimension of species vulnerability is their sensitivity to changes in climatic conditions (i.e. the extent to which performance, persistence, fitness, and survival is dependent on prevalent climates; Dawson et al. 2011). Primate populations can be sensitive to climatic stress in many forms (Kamilar and Beaudrot 2018). For example, mechanistic models show that warmer temperatures might increase the metabolic rates of mouse lemurs (genus *Microcebus*), enhancing energetic costs and affecting important processes such as reproduction and growth (Lovegrove et al. 2014). In hibernating lemurs (e.g. *Cheirogaleus*), warmer temperatures can increase the temperature of the hibernacula, accelerating the depletion of energetic reserves and hence impacting the condition of animals when they come out of hibernation (Blanco et al. 2018). Indirect effects are also crucial. For example, climatic fluctuations and extreme climatic events affect food availability and distribution, leading to changes in behavior, diet, body size, and fertility rates (Kamilar and Beaudrot 2018; Korstjens and Hillyer 2016; Meyer 2017). Additionally, many primates exhibit life-history and spatial traits associated with higher extinction risk from climate change, such as large body size, long generation length, small ranges, or small population size (Pearson et al. 2014). However, a long-term study with seven primate species found a weak relationship between climate variability and survival rates for all species, although for three (*Brachyteles*

hypoxanthus, *Cercopithecus mitis*, and *Propithecus verreauxi*) fertility rates were strongly associated with climate variables (Campos et al. 2017).

Since most primates will be exposed to future climate change and evidence suggests that the group is sensitive to this threat, it is critical to evaluate whether primates will be able to adapt to the forthcoming changes. In general, populations can cope with climate change by either adapting *in situ* or dispersing to more suitable habitats (Bellard et al. 2012; Dawson et al. 2011). Although climate-driven range shifts are well documented worldwide (Pecl et al. 2017), moving to track suitable climatic conditions might be challenging for primates. In a recent study with 80 Amazon primates, Sales et al. (2019) showed that rivers would limit climate-driven dispersal for ~20% of the species analyzed, increasing from 26% to 48% the number of species predicted to experience climate-related range contractions under a mitigation scenario. When expected deforestation was included in the models, dispersal was even more constrained, increasing to 59% the number of species predicted to lose range area. If carbon emissions and deforestation remain unabated, this number could rise to >80% (Sales et al. 2019).

Natural anthropogenic barriers may not be the only factors limiting primate dispersal. As climate changes at accelerating rates, intrinsic dispersal limitations may also prevent primates from traveling fast enough to track their moving ecological niches (Sales et al. 2020; Schloss et al. 2012). Consequently, species might be confined to unsuitable sites, which means that their survival will depend on their ability to adapt *in situ*. Therefore, a more comprehensive picture of the extent to which primates are threatened by climate change depends on evaluating their capacity to adapt to these changes evolutionarily.

In this study, we used phylogenetic comparative methods and climate forecasts to estimate whether rates of climatic niche evolution in primates are faster or slower than projected climate change. Using a relatively comprehensive phylogeny, we identified pairs of sister species and reconstructed ancestral character states for six climatic variables. We then estimated how quickly primate climatic niches evolved since the speciation event, and compared these results with projected rates of climate change. We show that rates of climatic niche evolution are much slower than rates of climate change, even under a scenario of moderate change. These findings suggest that primate adaptation may depend on rates of climatic niche evolution much faster than those observed in the recent evolutionary history of the group.

Methods

Climatic, Phylogenetic, and Distribution Data

We extracted current climate data from the WorldClim 2.1 database (Fick and Hijmans 2017). We selected six climatic variables: annual mean temperature (AMT), maximum temperature of warmest month (TMAX), minimum temperature of coldest month (TMIN), temperature seasonality (TSEAS), annual precipitation (AP), and precipitation seasonality (PSEAS). In addition to being commonly used for describing climatic niches, these variables were chosen based on their relationship with primate species richness (e.g. AP; Wang et al. 2013), structure of primate communities (e.g. AP, PSEAS, and TSEAS; Kamilar 2009; Kamilar et al. 2014), geographical distribution of mammals (e.g. TMIN; Olalla-Tárraga et al. 2011), and extinction risk from climate change

(e.g. TMAX; Román-Palacios and Wiens 2020). Moreover, TMAX, TSEAS, and PSEAS are variables associated with extreme climatic events such as heat waves and droughts, which are an important component of primate vulnerability to climate change (Zhang et al. 2019).

We obtained future climate data for 2081-2100 from 8 global climate models developed for the Coupled Model Intercomparison Project 6 (CMIP6; Eyring et al. 2016): BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0. We analyzed two shared socio-economic pathways, a moderate mitigation (SSP245) and a high-emissions scenario (SSP585). We then calculated the mean of estimates across all models and used these values in the subsequent analyses. Current and future climate variables have a spatial resolution of 2.5 arc minutes (~5 km² at the equator).

Phylogenetic data were obtained from PHYLACINE version 1.2.1 (Faurby et al. 2018). PHYLACINE is a macroecological database which provides phylogenetic, distribution, and trait data for mammals. Their time-calibrated phylogeny is based on a heuristic-hierarchical Bayesian approach and includes >5800 taxa. However, we only considered the phylogeny for which genetic data was available for all species and topological placement was unambiguously based on taxonomical information. Importantly, PHYLACINE provides the posterior distribution of 1000 phylogenetic trees, allowing users to take into account phylogenetic uncertainty in topology and branch lengths. Given that our analyses of niche evolution are based on branch lengths, we were able to incorporate phylogenetic uncertainty in our estimates.

Although PHYLACINE also provides distribution data, we obtained primate distribution data from the IUCN Red List of Threatened Species version 2020-2 (IUCN, 2020), due to its finer spatial resolution (while IUCN provides distribution data as range

polygons, PHYLACINE rasterized range maps with a resolution of 96.5 km by 96.5 km). We only considered data from species classified as extant or possibly extant, and the origin was classified as native or reintroduced. However, for twelve species (*Alouatta seniculus*, *Callicebus aureipalatii*, *Callicebus baptista*, *Cebus aequatorialis*, *Cebus brunneus*, *Cebus capucinus*, *Cebus cesarae*, *Cebus malitiosus*, *Cebus versicolor*, *Cheirogaleus minusculus*, *Ptilocolobus temminckii*, and *Pithecia milleri*) distribution data were not available on the IUCN database. In these cases, we used data from PHYLACINE. We then summarized the climatic niche of each species by calculating the mean of each variable across their distribution range. In order to obtain a more complete representation, we summarized the climatic niche of each species in three ways, by calculating the mean, the 90% quantile, and the 10% quantile of each variable across their distribution range. This analysis was performed using the R package `RASTER` version 3.3-7 (Hijmans 2020) and the data are provided in Appendix S1.

While WorldClim 2.1 compiles climate data averaged mostly for the 1970-2000 period (Fick and Hijmans 2017), IUCN range maps include regions with current or recent (within the past 20-30 years) distribution records, as well as areas in which species are very likely to occur (IUCN 2020). Consequently, there is a slight temporal mismatch between the climate and geographical data. However, it is important to note that our estimates of rates of climatic niche evolution are based on interspecific variation, particularly variation between pairs of sister species (see below). Since most primates occur in tropical regions, species have recently experienced similar levels of warming. Therefore, differences between climatic niches of closely related species would probably remain similar. Moreover, to the best of our knowledge, there is little evidence that primate species have undergone significant climate-induced range shifts

in the past few decades. Therefore, we believe such mismatch is unlikely to bias our estimates.

For some species, there were divergences between the binomial names in the PHYLACINE and IUCN databases (Appendix S2). In these cases, we followed the IUCN nomenclature and updated the species names in the phylogenies accordingly. Species absent from the PHYLACINE database were excluded from the analyses due to the lack of phylogenetic information. We also excluded data from extinct species, as well as from humans. Our final dataset included climatic, phylogenetic, and distribution data for 367 species from 15 primate families.

Rates of climatic niche evolution

We estimated rates of climatic niche evolution following Quintero and Wiens (2013), Cang et al. (2016), and Jezkova and Wiens (2016). Firstly, we fitted four alternative models of trait evolution for each climatic variable: Brownian motion (BM; there is a linear accumulation of trait variance over evolutionary time), Ornstein-Uhlenbeck (OU; stabilizing selection around a single adaptive peak), white noise (WN; covariance among species due to phylogeny is equal to zero), and lambda (phylogenetic signal). We then used the Akaike information criterion corrected for small sample sizes (AICc) to calculate the weighted AICc and identify the best-fitting likelihood model. Models were fitted using the *fitContinuous* function in the R package GEIGER version 2.0.7 (Pennell et al. 2014). In order to incorporate phylogenetic uncertainty in our results, we repeated all analyses using the posterior distribution of the first 100 trees from PHYLACINE.

After identifying the best-fitting model, we reconstructed ancestral character states for each of the six climate variables across all phylogenies. Given that the best-fitting models were either OU or lambda (see results), we first applied the *rescale* function in `GEIGER` 2.0.7 to transform the branches of the trees following either an OU model (using the alpha parameter) or a lambda model (using the lambda parameter) (Cang et al. 2016; Olsen 2015). We then used the *reconstruct* function in the R package `APE` version 5.4 (Paradis and Schliep 2019) to estimate ancestral character states for each species, choosing the single stationary peak method when the best-fitting model was OU, and the generalized least squares method when the best-fitting model was lambda (Royer-Carenzi and Didier 2016). In order to account for the uncertainty in ancestral character reconstructions, we also computed the 95% confidence interval for all estimates and used these values to calculate rates of niche evolution.

Following standard practice, our niche evolution analyses focused only on sister species, as estimates for distantly related species may be problematic (Cang et al. 2016; Quintero and Wiens 2013). Furthermore, ancestral reconstructions are more prone to uncertainty for deeper nodes the phylogeny (Cunningham et al. 1998). To calculate rates of niche evolution, we took the absolute difference between the current climatic value of each species and the estimated value of the species pair's most recent ancestor, and divided by the age of the species. To summarize the results, we calculated the median of the estimates of niche evolution for each species across all phylogenies. These analyses were repeated using both the upper and lower bounds of the 95% confidence interval around ancestral state estimates. Because of the potential differences in the topology of the phylogenies, a pair of sister species found in one tree may not be found in other. However, this is not an issue for our analyses, since we are mainly interested in general

patterns within each family. Pairs of sister species retrieved from each phylogenetic tree are shown in Appendix S3.

Rates of future climate change

To obtain rates of future climate change, we first calculated the mean values of each climate variable across the current distribution range of each species, for both emission scenarios (SSP245 and SSP585). Calculations were performed using RASTER 3.3-7. We then calculated future rates of change as the absolute difference between current and future projections, divided by 105 years, which is the difference between 2090 (midpoint of 2081-2100) and 1985 (midpoint of 1970-2000). Again, we calculated the median of the estimates of future rates of climate change for all species within each family, using both emission scenarios.

To identify in which regions species may be at greater risk, we spatially mapped the geographical distribution of rates of climatic niche evolution and rates of future climate change. In order to obtain a general overview of rate variation, we merged the results obtained for all climatic variables into a single bivariate map. To this end, we first combined past and future rates estimated for each species into one dataset and transformed these values into z-scores. This transformation is important because variables differ in their units of measurement. We then assigned the transformed values to the range map of each species, overlaid all range maps, and calculated the mean value for each grid cell in the map. To obtain the final maps, we again overlaid the maps generated for each variable, and calculated the mean for each grid cell. We then classified the continuous rates into three categories using Jenks optimization method (Jenks 1967). This analysis was carried out using the mean value to summarize species

niches, since it represents an intermediate level of change (see Figs. 1-2). Maps were generated using the R package `BISCALE` 0.2.0 (Prener et al. 2020).

Given the wide variation between past rates of climatic niche evolution and future rates of climate change (Table 1), we log₁₀-transformed the rates prior to all graphical analyses. All analyses were carried out in R version 4.0.2 (R Core Team 2020).

Data availability

All data used in this study are accessible through public databases described in the Methods section. All results obtained are included in this published article (and its online supplementary information). The R codes used in the analyses are available from the corresponding author on reasonable request.

Results

The evolutionary models that best described the climatic niche evolution in our data set were either OU or lambda. For temperature-related variables, OU was usually the best-fitting model of evolution. Conversely, for precipitation-related variables, lambda was the best-fitting model for all phylogenies. Values of AICc and weighted AICc used to select the best-fitting models are provided in Appendices S4 and S5, respectively.

We obtained rate estimates for 293 species across all 15 families. We find that for all species, rates of climatic niche evolution were much slower than rates of future climate change (Figs. 1-2 and Table 1). Overall, differences between rates were more pronounced for AMT, TMAX, and TMIN (Fig. 1). Variation in rates of evolution within families were generally greater than between families. Overall, past rates of niche

evolution tended to be similar regardless of the way we measured the niche of the species (i.e. mean, 10% quantile or 90% quantile; Figs. 1-2). However, future rates tended to be faster for the lower boundaries of the niche, and slower for the upper boundaries (Figs. 1-2). These patterns were very similar when rates were estimated using either the upper or lower bounds of the 95% confidence interval around ancestral state estimates (Appendices S6 and S7). Full results are provided in Appendices S8-S13.

In order to provide an overall picture of the difference between past and future rates for each variable, we treated the results obtained across all methods as a single dataset. We then calculated the median estimated rate of niche evolution for each variable, as well as the projected rate of climate change relative to rates of niche evolution among species. These results are presented in Table 1. Individual results for each method used to summarize climatic niches and reconstruct ancestral characters are presented in Appendices S14-S16. For temperature-related variables, the median rate of climatic niche evolution varied between 0.7-1.7 °C Myr⁻¹. Rates of niche evolution were faster for TMIN and slower for TMAX (Table 1). For the moderate emission scenario (SSP245), the variable that showed the smaller difference between past and future rates was TSEAS, with the expected rates of change being approximately 2,800 times faster than rates of niche evolution. On the other hand, TMAX showed the highest difference (future rates roughly 38,000 times faster than past rates). Under the high emission scenario, the discrepancy is higher for all variables, varying between ~4,800 times (TSEAS) to ~71,500 times (TMAX). However, substantial deviations from the median were observed (Table 1), reflecting the strong variation in rates within families.

Figure 3 shows how rates of climatic niche evolution are distributed across one of the phylogenies used in this study. In general, rates are relatively equally distributed, with most species presenting low to moderate rates for all variables, except for PSEAS.

Considering all variables, only a few species show disproportionately fast rates. These are mostly concentrated in the parvorder Catarrhini, especially in the family Cercopithecidae. However, even for these species past rates are much slower than future rates (Figs. 1-2, Appendices S7-S12). The magnitude of rates observed for precipitation and temperature-related variables seem to be decoupled. In other words, evolutionary change can be fast for temperature but slow for precipitation, and vice-versa. However, the substantial variation in rates observed within families (Figs. 1-2, Table 1) indicates that these results are influenced by both tree topology and branch length, highlighting the importance of considering phylogenetic uncertainty.

The bivariate map (Fig. 4) shows that past rates are comparatively faster in most of South and Southeast Asia, North and South Sub-Saharan Africa, Northeast and Southeast South America, and some scattered areas in Amazonia and the Malay Archipelago. On the other hand, future rates are faster in most parts of the Americas (especially in Central South America), Southeast Asia, most of the Malay Archipelago, and throughout Africa, especially in central and eastern regions.

Discussion

Growing evidence suggests that primates might be particularly vulnerable to future climate change, given their life-history traits, exposure, and sensitivity to climatic conditions. Therefore, a critical question is whether they can evolutionarily adapt to projected changes. In this study, we estimate rates of climatic niche evolution among primate species and compare these with rates of climate change expected by the end of the century. We find that rates of climatic niche evolution are invariably much slower than rates of future climate change. Even under a moderate scenario (SSP245), past and

future rates differ by at least 2,800-fold for temperature-related variables and 6,700-fold for precipitation-related variables. Results were similar for all 15 families analyzed, indicating that primates, as a whole, are likely to experience negative effects from climate change. Species occurring in Central South America, Central and Eastern Africa, Southeast Asia, and the Malay Archipelago will experience the fastest rates of future climate change. Overall, these findings suggest that primate adaptation to future climate change may require rates without parallel in the recent evolutionary history of the group. Despite having important implications for primate vulnerability, we emphasize that these results should be interpreted taking into account the assumptions and caveats of our analyses.

Our findings are in agreement with a growing body of evidence that shows that species are able to adapt *in situ* to ongoing climate change. For instance, climate-related range shifts are already widespread across taxa and ecosystems (Gottfried et al. 2012; Lenoir and Svenning 2015; Pecl et al. 2017; Poloczanska et al. 2016). Population declines due to climate change are also increasingly documented (Iknayan and Beissinger 2018; Martay et al. 2017; Soroye et al. 2020), as well as local extinctions (Wiens 2016). Such extinctions were usually associated with changes in TMAX (Román-Palacios and Wiens 2020), the variable with the highest difference between past and future rates (Table 1). Therefore, it is safe to speculate that many species are already failing to adapt *in situ*, even though recent changes have occurred at a slower rate than that expected for the next decades. Worryingly, even populations showing adaptive responses to climate change may not be able to persist given the fast pace of changes underway (Radchuk et al. 2019).

The results presented here are also consistent with earlier studies that investigated climatic niche evolution in primates and other vertebrates. A similar

analysis with 540 vertebrate species showed that the mean rate of climatic niche evolution for annual mean temperature was $1.34\text{ }^{\circ}\text{C Myr}^{-1}$ (Quintero and Wiens 2013). For primates, estimated median rate varied between $0.9 \pm 0.9\text{ }^{\circ}\text{C Myr}^{-1}$ (Table 1). These slightly slower rates were also observed in other tropical species (Jezkova and Wiens 2016; Lawson and Weir 2014), and might be explained by the narrow historical variability of tropical climates (Mora et al. 2013) and the reduced temperature niche breadth observed in low latitudes (Vázquez and Stevens 2004). A study with New World monkeys (Platyrrhini) demonstrated that different climatic niche axes exhibit heterogeneous patterns of niche evolution (Duran et al. 2013). Accordingly, we show that rates of climatic niche evolution vary across variables, especially when we compare the magnitude of rates in temperature-related variables (Table 1, Fig. 3). Duran and Pie (2015) showed that shifts in rates of climatic niche evolution are more frequent in Catarrhini. These results match our findings that most of the species with disproportionately fast rates are Catarrhini primates.

However, it is important to emphasize that one cannot draw final conclusions about the fate of primates based solely on our analyses, as species can avoid or mitigate negative effects through mechanisms other than niche evolution (Bellard et al. 2012). For example, evidence that primates may not be able to shift their distributions fast enough to track moving climates come mainly from studies with New World monkeys (e.g. Sales et al. 2020; Schloss et al. 2012). However, most New World monkeys are fully arboreal species (McCabe 2017), and therefore exhibit a low capacity to cross biogeographical barriers or move through human-altered landscapes. Consequently, range shifts might still be an alternative for semiarboreal or terrestrial primates, although this hypothesis remains untested. Physiological and behavioral plasticity may also play an important role in climate change adaptation (Lavergne et al. 2010; van

Schaik 2013), yet little is known about the extent to which mammals could adapt through these mechanisms (Boutin and Lane 2014). The lack of a clear relationship between climate variability and primate survival rates also suggests that fluctuating climatic conditions could be buffered by some species (Campos et al. 2017). However, fertility rates can still be strongly impacted by climatic changes, especially due to extreme events such as droughts (Campos et al. 2017; 2020), thus increasing the risk of climate-related population declines.

Extreme climatic events are also an important driver of change in future rates of climate change for several primates. A recent analysis showed that 16% and 22% of all primates are vulnerable to cyclones and droughts, respectively (Zhang et al. 2019), and these numbers may increase as extreme events are predicted to become more frequent and/or intense. Our results indicate that some of the hotspots of primate vulnerability to extreme events coincide with areas in which future rates of future climate change will be disproportionately faster than rates of climatic niche evolution. For example, cyclone-vulnerable primates are mainly distributed across Mesoamerica, Madagascar, East and Southeast Asia (Zhang et al. 2019). Drought-vulnerable primates are also found in Mesoamerica and Madagascar, as well as Central Africa, South and Southeast Asia. In all of these regions, rates of future rates comparatively faster (Fig. 4). Although some of variables we used are associated with extreme climate events (e.g. TMAX, TSEAS, and PSEAS), our predictions may be over conservative for the species and populations inhabiting these areas.

Finally, our analyses are subject to several caveats that have already been extensively discussed elsewhere (Jezkova and Wiens 2016; Quintero and Wiens 2013). We will briefly address some of them here. Firstly, our estimates are based solely on realized niches, which might result in an incomplete characterization of species' climatic

niches. If a species has a broader fundamental niche, rates of future climatic niche evolution would be slower. However, given the dramatic differences between past and future rates observed here, it is unclear whether broader fundamental niches would prevent species from being affected by climate change. Another important caveat is that we assume that rates of climatic niche evolution are constant over time. We acknowledge that, for several traits, as evolution can occur rapidly over short periods of time (Gingerich 2009), so can shifts in climatic niches (Wiens et al. 2019). Yet, rapid climatic niche shifts may be limited by biotic interactions (Wiens et al. 2019). Climate-related changes in biotic interactions are an important cause of population declines and local extinctions (Cahill et al. 2013), and empirical studies demonstrated that they are related with population declines in primates, especially after extreme weather events (Campos et al. 2017, 2020; Kamilar and Beaudrot 2018). Therefore, we believe that this is a reasonable assumption. Finally, local adaptation is also an important factor, which can increase rates of evolution among populations (Jezkova and Wiens 2016). However, even if primate populations show faster rates of evolution than those observed here, it is uncertain whether they will be able to keep up with projected rates of climate change and their synergy with other ongoing threats.

Conflict of Interest: The authors declare that they have no conflict of interest.

References

Barrett, M. A., Brown, J. L., Junge, R. E., & Yoder, A. D. (2013). Climate change, predictive modeling and lemur health: Assessing impacts of changing climate on health and

conservation in Madagascar. *Biological Conservation*, 157, 409–422.

<https://doi.org/https://doi.org/10.1016/j.biocon.2012.09.003>

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365–377.

<https://doi.org/10.1111/j.1461-0248.2011.01736.x>

Blanco, M. B., Dausmann, K. H., Faherty, S. L., & Yoder, A. D. (2018). Tropical heterothermy is “cool”: The expression of daily torpor and hibernation in primates. *Evolutionary Anthropology*, 27(4), 147–161. <https://doi.org/10.1002/evan.21588>

Boutin, S., & Lane, J. E. (2014). Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications*, 7(1), 29–41.

<https://doi.org/10.1111/eva.12121>

Brown, J. L., & Yoder, A. D. (2015). Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution*, 5(6), 1131–1142.

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., et al. (2013). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), 20121890.

<https://doi.org/10.1098/rspb.2012.1890>

Campos, F. A., Kalbitzer, U., Melin, A. D., Hogan, J. D., Cheves, S. E., Murillo-Chacon, E., et al. (2020). Differential impact of severe drought on infant mortality in two sympatric neotropical primates. *Royal Society Open Science*, 7(4).

<https://doi.org/10.1098/rsos.200302>

Campos, F. A., Morris, W. F., Alberts, S. C., Altmann, J., Brockman, D. K., Cords, M., et al. (2017). Does climate variability influence the demography of wild primates?

Evidence from long-term life-history data in seven species. *Global Change Biology*, 23(11), 4907–4921. <https://doi.org/10.1111/gcb.13754>

Cang, F. A., Wilson, A. A., & Wiens, J. J. (2016). Climate change is projected to outpace rates of niche change in grasses. *Biology Letters*, *12*(9), 20160368.

<https://doi.org/10.1098/rsbl.2016.0368>

Carvalho, J. S., Graham, B., Rebelo, H., Bocksberger, G., Meyer, C. F. J., Wich, S., & Köhl, H. S. (2019). A global risk assessment of primates under climate and land use/cover scenarios. *Global Change Biology*, *25*(9), 3163–3178.

<https://doi.org/10.1111/gcb.14671>

Coumou, D., & Rahmstorf, S. (2012). A decade of weather extremes. *Nature Climate Change*, *2*(7), 491–496. <https://doi.org/10.1038/nclimate1452>

Cunningham, C. W., Omland, K. E., & Oakley, T. H. (1998). Reconstructing ancestral character states: a critical reappraisal. *Trends in Ecology & Evolution*, *13*(9), 361–366. [https://doi.org/https://doi.org/10.1016/S0169-5347\(98\)01382-2](https://doi.org/https://doi.org/10.1016/S0169-5347(98)01382-2)

Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond predictions: Biodiversity conservation in a changing climate. *Science*, *332*(6025), 53–58. <https://doi.org/10.1126/science.1200303>

Duran, A., Meyer, A. L. S., & Pie, M. R. (2013). Climatic niche evolution in New World monkeys (Platyrrhini). *PLoS ONE*, *8*(12), e83684.

<https://doi.org/10.1371/journal.pone.0083684>

Duran, A., & Pie, M. R. (2015). Tempo and mode of climatic niche evolution in Primates. *Evolution*, *69*(9), 2496–2506. <https://doi.org/https://doi.org/10.1111/evo.12730>

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Fiore, A. Di, et al. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), e1600946. <https://doi.org/10.1126/sciadv.1600946>

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. E.

(2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6)

- experimental design and organization. *Geoscientific Model Development*, 9(5), 1937–1958. <https://doi.org/10.5194/gmd-9-1937-2016>
- Faurby, S., Davis, M., Pedersen, R., Schowanek, S. D., Antonelli, A., & Svenning, J. C. (2018). PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology*, 99(11), 2626. <https://doi.org/10.1002/ecy.2443>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology*, 37(12), 4302–4315.
- Gingerich, P. D. (2009). Rates of Evolution. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 657–675. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173457>
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., et al. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), 111–115. <https://doi.org/10.1038/nclimate1329>
- Gouveia, S. F., Souza-Alves, J. P., Rattis, L., Dobrovolski, R., Jerusalinsky, L., Beltrão-Mendes, R., & Ferrari, S. F. (2016). Climate and land use changes will degrade the configuration of the landscape for titi monkeys in eastern Brazil. *Global Change Biology*, 22(6), 2003–2012. <https://doi.org/10.1111/gcb.13162>
- Graham, T. L., Matthews, H. D., & Turner, S. E. (2016). A Global-Scale Evaluation of Primate Exposure and Vulnerability to Climate Change. *International Journal of Primatology*, 37(2), 158–174. <https://doi.org/10.1007/s10764-016-9890-4>
- Hijmans, R. J. (2020). raster: Geographic Data Analysis and Modeling. R package version 3.3-7. <https://cran.r-project.org/package=raster>
- Hill, S. E., & Winder, I. C. (2019). Predicting the impacts of climate change on *Papio* baboon biogeography: Are widespread, generalist primates ‘safe’? *Journal of*

Biogeography, 46(7), 1380–1405. <https://doi.org/10.1111/jbi.13582>

Ikcnayan, K. J., & Beissinger, S. R. (2018). Collapse of a desert bird community over the past century driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 115(34), 8597–8602.

<https://doi.org/10.1073/pnas.1805123115>

IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. (R. K. P. and L. A. M. Core Writing Team, Ed.) *IPCC 5th Assessment Report*.

IUCN. (2020) The IUCN Red List of Threatened Species. Version 2020-2.

<https://www.iucnredlist.org>. Downloaded on March 9th 2020.

Jenks, G. F. (1967). The data model concept in statistical mapping. *International Yearbook of Cartography*, 7, 186–190.

Jezkova, T., & Wiens, J. J. (2016). Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proceedings of the Royal Society B: Biological Sciences*, 283(1843).

<https://doi.org/10.1098/rspb.2016.2104>

Kamilar, J. M. (2009). Environmental and geographic correlates of the taxonomic structure of primate communities. *American Journal of Physical Anthropology*, 139(3), 382–393. <https://doi.org/10.1002/ajpa.20993>

Kamilar, J. M., & Beaudrot, L. (2018). Effects of environmental stress on primate populations. *Annual Review of Anthropology*, 47, 417–434.

<https://doi.org/10.1146/annurev-anthro-102317-045949>

Kamilar, J. M., Beaudrot, L., & Reed, K. E. (2014). The Influences of Species Richness and Climate on the Phylogenetic Structure of African Haplorhine and Strepsirrhine Primate Communities. *International Journal of Primatology*, 35, 1105–1121.

<https://doi.org/10.1007/s10764-014-9784-2>

Korstjens, A. H., & Hillyer, A. P. (2016). Primates and climate change: a review of current knowledge. In S. A. Wich & A. J. Marshall (Eds.), *An Introduction to Primate Conservation* (pp. 175–192). Oxford University Press (OUP).

<https://doi.org/10.1093/acprof:oso/9780198703389.003.0011>

Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 321–350.

<https://doi.org/10.1146/annurev-ecolsys-102209-144628>

Lawson, A. M., & Weir, J. T. (2014). Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters*, *17*(11), 1427–1436.

<https://doi.org/10.1111/ele.12346>

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28.

<https://doi.org/https://doi.org/10.1111/ecog.00967>

Lenoir, Jonathan, Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, 1–16.

<https://doi.org/10.1038/s41559-020-1198-2>

Lovegrove, B. G., Canale, C., Levesque, D., Fluch, G., Řeháková-Petrů, M., & Ruf, T. (2014). Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? *Physiological and Biochemical Zoology*, *87*(1), 30–45.

<https://doi.org/10.1086/673313>

Martay, B., Brewer, M. J., Elston, D. A., Bell, J. R., Harrington, R., Brereton, T. M., et al. (2017). Impacts of climate change on national biodiversity population trends.

Ecography, 40(10), 1139–1151.

<https://doi.org/https://doi.org/10.1111/ecog.02411>

MCabe, S. C. J. (2017). Arboreal Locomotion. In F. A. Bezanson M., MacKinnon K. C., Riley E., Campbell C.J., Nekaris A. K.I., Estrada A, Di Fiore A.F., Ross S., Jones-Engel L.E., Thierry B., Sussman R.W., Sanz C., Loudon J., Elton S. (Ed.), *The International Encyclopedia of Primatology* (pp. 1–2).

<https://doi.org/https://doi.org/10.1002/9781119179313.wbprim0335>

Meyer, A. L. S. (2017). Climate Change, Forests, and Primate Conservation. In M. Bezanson; K.C. MacKinnon; E. Riley; C.J. Campbell; K.I. Nekaris; A. Estrada; A.F. Di Fiore; S. Ross; L.E. Jones-Engel; B. Thierry; R.W. Sussman; C. Sanz; J. Loudon; S. Elton; A. Fuentes (Ed.), *The International Encyclopedia of Primatology* (pp. 1–6).

<https://doi.org/10.1002/9781119179313.wbprim0284>

Meyer, A. L. S., Pie, M. R., & Passos, F. C. (2014). Assessing the exposure of lion tamarins (*Leontopithecus* spp.) to future climate change. *American Journal of Primatology*, 76(6), 551–562. <https://doi.org/10.1002/ajp.22247>

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., et al. (2013). The projected timing of climate departure from recent variability. *Nature*, 502(7470), 183–187. <https://doi.org/10.1038/nature12540>

Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology and Evolution*, In press.

<https://doi.org/10.1038/s41559-020-01303-0>

Olalla-Tárraga, M. Á., McInnes, L., Bini, L. M., Diniz-Filho, J. A. F., Fritz, S. A., Hawkins, B. A., et al. (2011). Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. *Journal of*

Biogeography, 38(12), 2237–2247.

<https://doi.org/10.1111/j.1365-2699.2011.02570.x>

Olsen, A. M. (2015). Exceptional avian herbivores: multiple transitions toward herbivory in the bird order Anseriformes and its correlation with body mass. *Ecology and Evolution*, 5(21), 5016–5032. <https://doi.org/10.1002/ece3.1787>

Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, 7(3), 205–208. <https://doi.org/10.1038/nclimate3223>

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528.

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., et al. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, 4(3), 217–221.

<https://doi.org/10.1038/nclimate2113>

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., et al. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*. <https://doi.org/10.1126/science.aai9214>

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., et al. (2014). geiger v2. 0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics*, 30(15), 2216–2218.

Poloczanska, E. S., Burrows, M. T., Brown, C. J., Molinos, J. G., Halpern, B. S., Hoegh-Guldberg, O., et al. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*.

<https://doi.org/10.3389/fmars.2016.00062>

Prener, C., Grossenbacher, T., & Zehr, A. (2020). biscale: Tools and Palettes for Bivariate

Thematic Mapping. R package version 0.2.0.

<https://cran.r-project.org/package=biscale>

Quintero, I., & Wiens, J. J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecology Letters*, *16*(8), 1095–1103. <https://doi.org/10.1111/ele.12144>

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>

Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., et al. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, *10*(1), 1–14. <https://doi.org/10.1038/s41467-019-10924-4>

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(8), 4211–4217. <https://doi.org/10.1073/pnas.1913007117>

Royer-Carenzi, M., & Didier, G. (2016). A comparison of ancestral state reconstruction methods for quantitative characters. *Journal of Theoretical Biology*, *404*, 126–142. <https://doi.org/10.1016/j.jtbi.2016.05.029>

Sales, L. P., Ribeiro, B. R., Chapman, C. A., & Loyola, R. (2020). Multiple dimensions of climate change on the distribution of Amazon primates. *Perspectives in Ecology and Conservation*, *18*(2), 83–90. <https://doi.org/10.1016/j.pecon.2020.03.001>

Sales, L. P., Ribeiro, B. R., Pires, M. M., Chapman, C. A., & Loyola, R. (2019). Recalculating route: dispersal constraints will drive the redistribution of Amazon primates in the Anthropocene. *Ecography*, *42*(10), 1789–1801.

<https://doi.org/10.1111/ecog.04499>

Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(22), 8606–8611.

<https://doi.org/10.1073/pnas.1116791109>

Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, *367*(6478), 685–688.

<https://doi.org/10.1126/science.aax8591>

Stewart, B. M., Turner, S. E., & Matthews, H. D. (2020). Climate change impacts on potential future ranges of non-human primate species. *Climatic Change*, *162*(4), 2301–2318. <https://doi.org/10.1007/s10584-020-02776-5>

Trisos, C. H., Merow, C., & Pigot, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, *580*(7804), 496–501.

<https://doi.org/10.1038/s41586-020-2189-9>

van Schaik, C. P. (2013). The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120339.

<https://doi.org/10.1098/rstb.2012.0339>

Vázquez, D. P., & Stevens, R. D. (2004). The latitudinal gradient in niche breadth: concepts and evidence. *The American naturalist*, *164*(1), E1–E19.

<https://doi.org/10.1086/421445>

Wang, Y.-C., Srivathsan, A., Feng, C.-C., Salim, A., & Shekelle, M. (2013). Asian Primate Species Richness Correlates with Rainfall. *PLoS ONE*, *8*(1), e54995.

<https://doi.org/10.1371/journal.pone.0054995>

Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among

Plant and Animal Species. *PLOS Biology*, 14(12), e2001104.

<https://doi.org/10.1371/journal.pbio.2001104>

Wiens, J. J., Litvinenko, Y., Harris, L., & Jezkova, T. (2019). Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change. *Journal of Biogeography*, 46(9), 2115–2125.

<https://doi.org/https://doi.org/10.1111/jbi.13649>

Zhang, L., Ameca, E. I., Cowlshaw, G., Pettorelli, N., Foden, W., & Mace, G. M. (2019).

Global assessment of primate vulnerability to extreme climatic events. *Nature Climate Change*, 9(7), 554–561. <https://doi.org/10.1038/s41558-019-0508-7>

Figure legends:

Figure 1: Ridgeline plots showing the distribution of estimated rates of climatic niche evolution and estimated rates of future climate change for 15 primate families. Results are shown for annual mean temperature, maximum temperature of the warmest month, and minimum temperature of the coldest month. Estimates are classified according to the methods used to summarize the climatic niche of each species (i.e. mean, 10% quantile, and 90% quantile). Darker colors represent rates of future climate change. The left column shows estimates for the moderate mitigation scenario (SSP245). The right column shows estimates for the high emissions scenarios (SSP585).

Figure 2. Continuation of Fig. 1 showing results for temperature seasonality, annual precipitation, and precipitation seasonality.

Figure 3: Median rates of climatic niche evolution for each species next to one of the phylogenies used to estimate the rates. Rates were estimated for six climatic variables: annual mean temperature (AMT), maximum temperature of warmest month (TMAX), minimum temperature of coldest month (TMIN), temperature seasonality (TSEAS), annual precipitation (AP), and precipitation seasonality (PSEAS). The units on the axes are given as $^{\circ}\text{C Myr}^{-1}$ for AMT, TMAX, and TMIN, (standard deviation $\times 100$) $^{\circ}\text{C Myr}^{-1}$ for TSEAS, mm Myr^{-1} for AP, and (coefficient of variation) mm Myr^{-1} for PSEAS.

Figure 4. The geographical distribution of estimated rates of climatic niche evolution and estimated rates of future climate change.

Table 1. Summary of rates of climatic niche evolution estimated for each variable and both emission scenarios. Rates were obtained for each method used to summarize climatic niches and reconstruct ancestral characters, and then treated as a single dataset. Values of climatic niche evolution are based on the median for all species across all methods. Values of relative rates indicate how many times higher the projected rate of climate change is relative to median rate of niche evolution. Corresponding values of median absolute deviation (MAD) are also presented.

Variable	Niche evolution		Projected change			
	Median	MAD	Moderate emission (SSP245)	MAD (SSP245)	High emission (SSP585)	MAD (SSP585)
AMT	0.9 °C Myr ⁻¹ 59.7 SD x 100	±0.9	26,532	±24,038	49,498	±45,306
TSEAS	Myr ⁻¹	±51	2,833	±3,460	4,813	±5,357
TMAX	0.7 °C Myr ⁻¹	±0.7	37,899	±34,152	71,555	±62,970
TMIN	1.7 °C Myr ⁻¹	±1.6	13,991	±13,728	24,993	±23,649
AP	194 mm Myr ⁻¹	±19	10,560	±11,559	11,682	±13,196
PSEAS	9.8 CV Myr ⁻¹	±9.5	6,717	±8,979	7,929	±9,340

Supplementary material:

Appendix S1: Mean, 90 quantile, and 10% quantile climatic niche estimates for all primates species used in this study.

Appendix S2: Comparison of species names between the PHYLACINE 1.2.1 database (phylogenetic data) and IUCN 2020-2 (geographic distribution data). In this study, we followed the nomenclature from the IUCN database.

Appendix S3. List of pairs of sister species used to estimate past rates of climatic niche evolution.

Appendix S4. Values of Akaike information criterion corrected for small sample sizes (AICc) used to calculate the weighted AICc for each variable in each phylogenetic tree.

Appendix S5. Values of weighted AICc used identify the best-fitting likelihood model.

Appendix S6. Comparison between estimated rates of climatic niche evolution and estimated rates of future climate change for 15 primate families. Results are shown for all variables. Here, niche rates were estimated from the upper bound of the ancestral character reconstruction 95% confidence interval. Full legend in Figure 1.

Appendix S7. Comparison between estimated rates of climatic niche evolution and estimated rates of future climate change for 15 primate families. Results are shown for

all variables. Here, niche rates were estimated from the lower bound of the ancestral character reconstruction 95% confidence interval. Full legend in Figure 1.

Appendices S8-S13. Full results for all variables.

Appendix S14. Summary of rates of climatic niche evolution estimated for each variable and the respective relative rates of future climate change. Climatic niches were estimated using the mean of each variable across the distribution range of the species. Results are shown for both emission scenarios and also include estimates from the bounds of the 95% confidence interval. Values of climatic niche evolution are based on the median for all species. Values of relative rates indicate how many times higher the projected rate of climate change is relative to median rate of niche evolution.

Corresponding values of median absolute deviation (MAD) are also presented.

Appendix S15. Summary of rates of climatic niche evolution estimated for each variable and the respective relative rates of future climate change. Climatic niches were estimated as the 90% quantile of each variable across the distribution range of the species. Results are shown for both emission scenarios and also include estimates from the bounds of the 95% confidence interval. Values of climatic niche evolution are based on the median for all species. Values of relative rates indicate how many times higher the projected rate of climate change is relative to median rate of niche evolution.

Corresponding values of median absolute deviation (MAD) are also presented.

Appendix S16. Summary of rates of climatic niche evolution estimated for each variable and the respective relative rates of future climate change. Climatic niches were

estimated as the 10% quantile of each variable across the distribution range of the species. Results are shown for both emission scenarios and also include estimates from the bounds of the 95% confidence interval. Values of climatic niche evolution are based on the median for all species. Values of relative rates indicate how many times higher the projected rate of climate change is relative to median rate of niche evolution. Corresponding values of median absolute deviation (MAD) are also presented.